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ORIGINAL ARTICLE

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## First record of an epibiosis between the sand crab *Emerita analoga* (Stimpson, 1857) (Decapoda: Hippidae) and the mussel *Semimytilus algosus* (Gould, 1850) (Bivalvia, Mytilidae) in southern Peru

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**Abstract** Coastal zones of the Humboldt Current Upwelling System (HCUS) are composed both of rocky and sandy beaches inhabited by macrozoobenthic communities. These show oscillating changes in the dominance of species; the abundance of the sand crab *Emerita analoga* is linked to phases of the El Niño Southern Oscillation (ENSO). The biogenic surfaces of these crabs serve as substrate for opportunistic colonizers. This study is the first record of an epibiosis between *E. analoga* and the rock mussel *Semimytilus algosus*, detected at a southern Peruvian sandy beach. Mussels fouled a wide size-range of adult *E. analoga* (7.3%) but they themselves belonged to small-size classes. The largest *S. algosus* was 17.4 mm in length. Highest permanence of epibionts was found on larger sand crabs (maximum between 24 and 27 mm). Significantly more mussels were found on the ventral surface (39.4%) compared to 10 other surface areas of the sand crab. Possible benefits and disadvantages of the observed epibiosis for both the basibiont and the epibiont are discussed.

**Keywords** Humboldt Current Upwelling System · Epibiosis · Fouling · *Semimytilus algosus* · *Emerita analoga*

### Introduction

The coastal Humboldt Current Upwelling System (HCUS) is one of the most productive marine ecosystems (Mann and Lazier 1991; Escribano et al. 1997; Marín et al. 2001). The system is fuelled by upwelling of nutrients, which stimulate the primary and secondary production (Escribano et al. 1997; Marín et al. 2001). Coastal zones of the HCUS consist of rocky as well as sandy beaches colonized by a diverse macroinfauna of invertebrates contributing to a high biomass (Soto 1985; Jaramillo et al. 1993; Arntz and Fahrback 1996). There are many studies on the patterns of macrofaunal zonation in exposed sandy beaches of the coastal upwelling system (e.g. Jaramillo et al. 1993, 2001; Jaramillo and McLachlan 1993), showing that changes in beach morphodynamic result in significant community responses of the intertidal macroinfauna. Communities of sandy beaches of south and central Peru show clear fluctuations of dominant species such as the surf clams *Mesodesma donacium* and *Donax marincovich*, and the sand crab *Emerita analoga*. The main reasons for these are natural climate variability as the El Niño Southern Oscillation (ENSO) (Tarazona et al. 1985; Arntz et al. 1987; Arntz and Fahrback 1996) and overexploitation.

The sand crab *E. analoga* (Crustacea, Anomura, Hippidae) is a widespread and abundant decapod inhabiting exposed sandy beaches of the Pacific coast (e.g. Contreras et al. 1999), and is a characteristic species of the swash zone (Jaramillo et al. 1993, 2001; Contreras et al. 1999). It can appear in high abundance forming aggregations at certain water temperatures, food availability and beach morphodynamics (Perry 1980; Dugan 1994; Jaramillo and McLachlan 1993; Contreras et al. 1999). The combination of substrate generalist characteristics and the unique orientation and swimming

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ability of *E. analoga* may be a key to its high abundance and wide distribution in the intertidal zone of exposed sandy beaches (Dugan et al. 1994, 2000). The hard carapace of this crab offers free substratum for species colonizing hard structures (Wahl 1989; Gili et al. 1993).

For metamorphoses and settlement the free-living larvae of sessile hard bottom invertebrates are highly dependent on the availability of a suitable substratum (Sebens 1985; Gili et al. 1993). The coastal area of northern Chile and southern to central Peru is dominated by soft bottom habitats, while rock substratum is scarce. Biogenic surfaces can also serve as settlement substrates resulting in epibiosis, a close association between two different species: a basibiont (the substrate organism) fouled by an epibiont (organism growing attached to a living surface; Wahl 1989). Host species reported from sandy beaches are mainly molluscs and crustaceans (Conover 1979; Warner 1997; Olabarria 2000), fouled by diverse sessile invertebrates. Such an association usually includes both benefits and disadvantages for epi- and basibiont (Wahl 1989; Gili et al. 1993), which have a more prominent effect under strong physical environmental conditions such as wave exposure and currents (Jackson 1977; Wahl 1989; Olabarria 2000). In southern Peru we observed that *E. analoga* was fouled by the rock mussel *Semimytilus algosus*, a common inhabitant of the low rocky intertidal fringe in central Chile, distributed between Ecuador and Chiloe-Island (approximately 42°S, Caro and Castilla 2004). The aim of this study was to describe this epibiosis and to discuss possible effects for both the host and the epibiont.

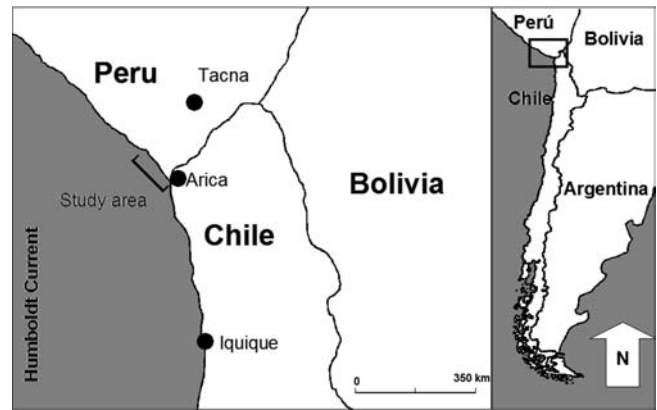
## Materials and methods

### Study area

This study was carried out at a large sandy beach (110 km) at the border between Chile (Arica) and Peru (Boca del Rio locality) (18°12'S; 70°35'W) (Fig. 1). The beach is fully exposed to the breaking waves resulting in the typical beach morphology with flat and steeper areas. Three faunal zones (upper, middle and lower shore) characterize these beaches, where *E. analoga* typically inhabits the lower shore (swash zone) along the Chilean coast. However, this sand crab was also found on the lower levels of the middle shore in the sandy beaches of Peru (McLachlan and Jaramillo 1995).

### Sampling and analysis

Sand crab *E. analoga* fouled by the mussel *S. algosus* were collected in the intertidal zone along the beach. Individuals of *E. analoga* covering the whole size range were sampled within a time period of 5 min each in two 100 m wide areas. The abundance of *E. analoga* in the



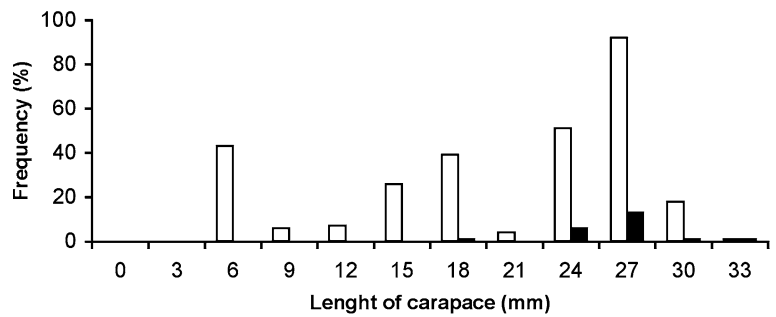
**Fig. 1** Map indicating the study area, which is part of the coastal Humboldt Current Upwelling System (18°12'S, 70°35'W) at the border between Chile and Peru

study area was determined using a cylindrical corer (10 cm in diameter). Individuals were fixed in 5% formalin. Thereafter individuals were measured (length of carapace) to the nearest 0.1 mm and observed under a binocular microscope in order to detect epibionts. Epibiotic mussels were identified and counted, their position on the basibiont was recorded and their length was measured. *S. algosus* was found attached to 11 different surface areas of *E. analoga* (see also Fig. 5): (1) ventral side, (2) right side of carapace, (3) inferior left maxilliped, (4) area between first and second pereopod, (5) anterior right edge of carapace, (6) dactylus of first pereopod, (7) superior pereopod left, (8) left side of carapace, (9) superior pereopod right, (10) dorsal carapace, (11) area between coxae and carapace. Images of fouled areas were taken using a digital camera (Canon G3—Power shot) and a binocular microscope (Carl Zeiss) with 230 magnification.

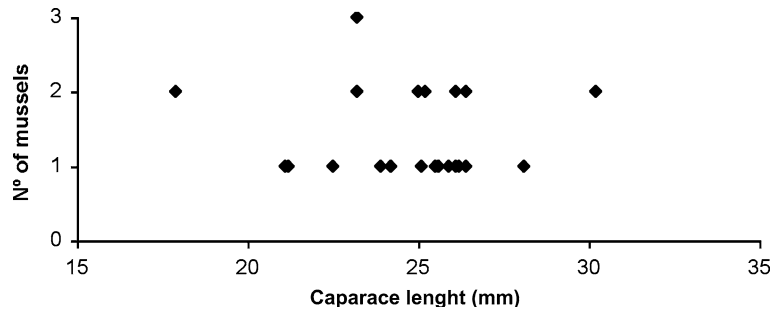
## Results

The abundance of *E. analoga* in the study area was 65 ind m<sup>-2</sup>. Among a total of 300 individuals of *E. analoga* analysed, 7.3% ( $n=22$ ) were fouled by *S. algosus*. These mussels were found on sand crabs ranging from 18 to 33 mm in carapace length, but mostly on crabs with 24 to 27 mm (Fig. 2). The highest number of epibionts per crab was three; however, most common was just one epibiont (Fig. 3). There was no clear relationship between the fouling intensity and the size of the basibiont ( $R^2=0.0065$ ). Fouling *S. algosus* ranged from 0.1 to 17.4 mm in anterior-posterior length (Fig. 4); smaller bivalves (below 5 mm shell length) were most abundant. Most mussels were found attached to zone 1 (39.4%) and zone 2 (18.2%); other zones of minor importance were zone 3 (9.1%) and zones 4–6, with 6.1% each (Fig. 5). Figure 6 illustrates the fouling of different surface areas of *E. analoga* by the mussel *S. algosus*.

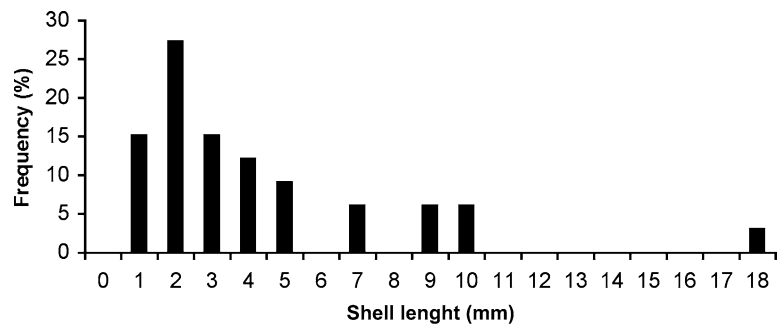
**Fig. 2** Size frequency distribution of the sand crab *E. analoga* without (*square box*) and with (*filled square box*) epibiotic mussels *S. algosus*, found at the large sandy beach between Arica and the Boca del Rio locality



**Fig. 3** Number of mussels *S. algosus* found on *E. analoga* as a function of the host's carapace length



**Fig. 4** Size frequency distribution of mussels *S. algosus* fouling the sand crab *E. analoga*

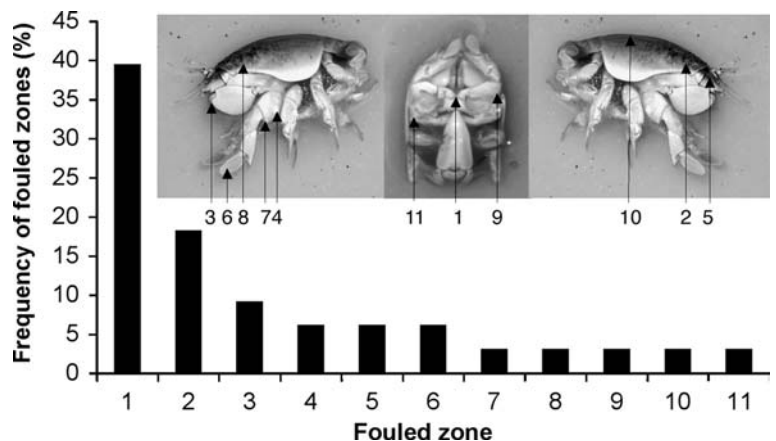


## Discussion

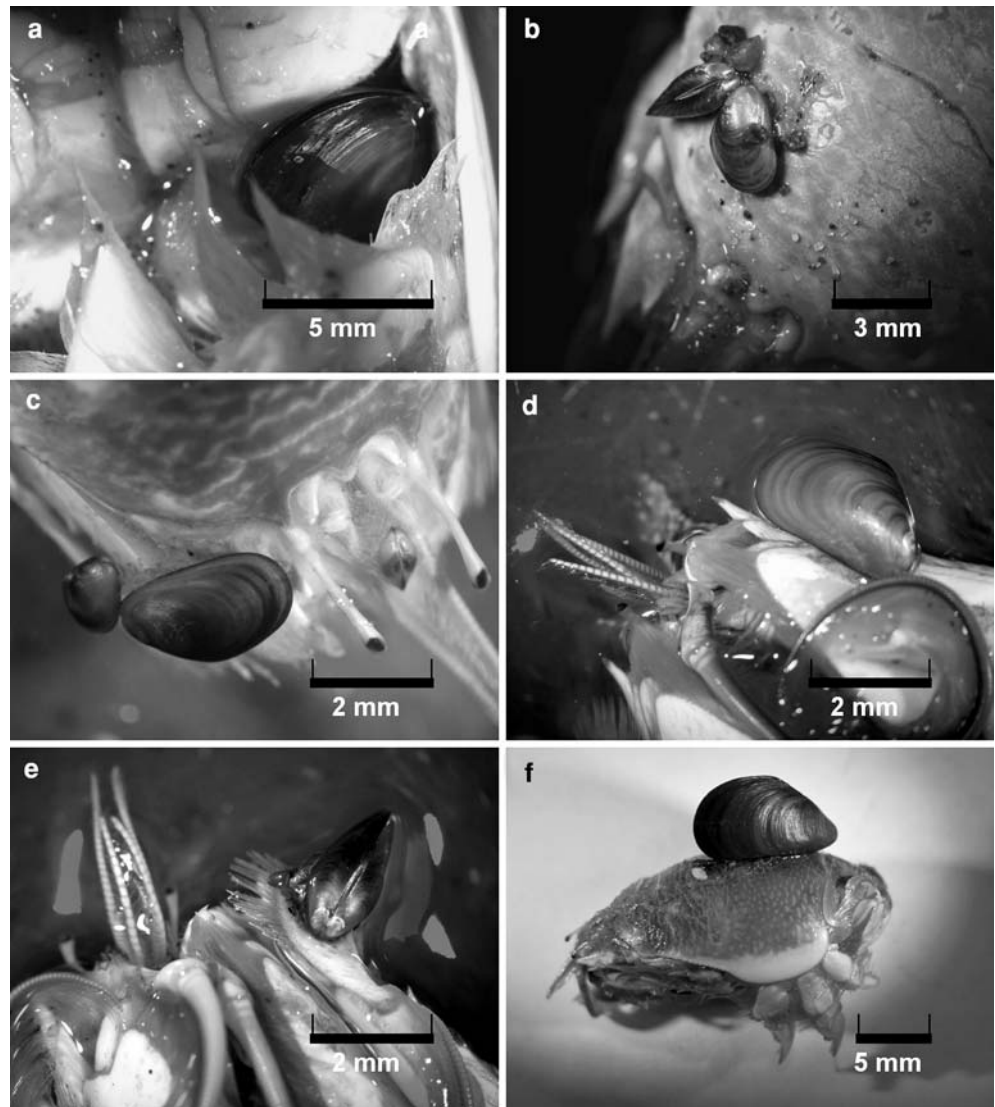
Biogenic substrates are commonly used as settling substrates by hard-bottom colonizers, especially in dynamic soft bottoms where no or only a few other substrates are available. This especially holds true for our study site, a

long highly exposed beach without solid rock. Hard bottom is very scarce over a long distance of coastline, apparently resulting in a high competition pressure for settling surfaces. Crustacean carapaces and shells of molluscs of different species were reported as potential substrates for colonizers in such soft-bottom habitats

**Fig. 5** Frequency distribution of mussels *S. algosus* attached to different surface areas (1–11) of its host *E. analoga*; inserted photographs (from left to right): left, ventral and right side of the host (see also Materials and methods)



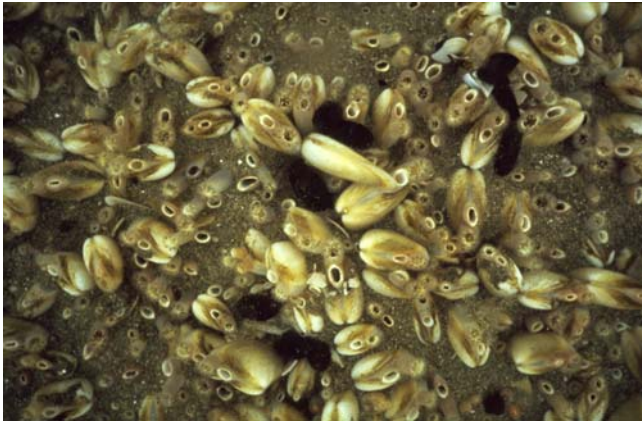
**Fig. 6** Photographs of mussels *S. algosus* fouling the crab *E. analoga*; **a** on the ventral surface between the pereopods, **b** on the right side of the carapace, **c** on the anterior right part of the carapace, **d** on the left inferior maxilliped, **e** distal on the first pereopod and **f** large mussel (17.4 mm) on the dorsal surface



(Conover 1979; Gili et al. 1993; Olabarría 2000). However, an association between the sand crab *E. analoga* and the rock mussels *S. algosus* has not yet been reported. The latter dominates exposed rocky intertidal communities in the low and middle latitudes of Pacific South America (Tokeshi and Romero 1995) and is recognized as an important primary colonizer in the HCUS (Tarazona et al. 1985; Tokeshi and Romero 1995). The larval phase of this mussel species varies from 17 to 20 days. Recruitment of *S. algosus* occurs throughout the year with major peaks in summer and, secondarily, winter months (June–August), showing interannual changes during EN (Navarrete et al. 2002).

Successful larval settlement and metamorphosis of Mytilidae depend on the availability of suitable substrata. Substrate choice is controlled by physical and biotic factors, with specific chemical stimuli for metamorphosis (e.g. living tissue of corals, Mokady et al. 1992; filamentous algae or filamentous structures, Davis and Moreno 1995). Under favourable substrate conditions, the larva crawls around for a certain

period of time, and then gradually stops moving in response to a hierarchy of stimuli; it protrudes its foot out of the shell and quickly secretes a single byssus thread, thereby attaching to the substrate (Lutz and Kennish 1992). Unlike the related mussel *Mytilus edulis*, which can form vast beds in soft-bottom habitats, for example, of the Baltic Sea (e.g. Schwenke 1969; Reusch 1994; Laudien and Wahl 1999), *S. algosus* is exclusively dependent on hard substrates. Besides bedrock, secondary hard bottoms such as the valves of the surf clam *M. donacium* can serve as substrate. Before EN 1982 *S. algosus* settled on a *M. donacium* bed in central Peru attaining densities of 281 ind m<sup>-2</sup> (Fig. 7). Although under unfavourable conditions the mussel can close its shells and survive several days (Schiedek and Currie 2002) *S. algosus* suffered a mass mortality when the clams were covered by sediment during a long period of strong swell (Arntz et al. 1987). Since EN 1998 *M. donacium* has not recovered former densities along the whole Peruvian coastline (Stotz et al. 2003).



**Fig. 7** Underwater photograph showing *S. algalus* settling on the surf clam *M. donacium* in central Peru before ENSO 1982

The sand crab *E. analoga* substituted the surf clams (Tarazona et al. 1985; Arntz et al. 1987) and became available as settlement substrate for the pioneer mussels. As a consequence mussels were observed fouling a wide size range of adult *E. analoga*. Most epibiotic mussels belonged to a correspondingly small-size class of probably young individuals. The highest permanence of epibionts was found on larger basibionts suggesting that bigger hosts offer more shelter and stability for the mussel to protect it from physical factors such as wave exposure. The evolutionary response of sessile basibionts to a potential epibiosis includes three classes of adaptations: tolerance, avoidance and defence (Wahl 1989). In crustaceans the mechanic defence such as the periodic renewal of the carapace due to moulting and the ‘sanding’ in dynamic high energy sandy beaches might regulate the colonization rate (Wahl 1989; Gili et al. 1993). Thus large-sized sand crabs might be more susceptible to fouling as the molt interval is longer and the crabs inhabit zones with more stable conditions.

Defence may be costly while tolerance entails both benefits and disadvantages for epi- and basibiont. According to Wahl and Mark (1999), specific and obligate epibionts are rare. Consequently, the majority of described associations are classified as facultative. The association between *E. analoga* and *S. algalus* probably involves a complex network of cost-benefit factors for the two species. In soft bottoms the opportunistic settlement of *S. algalus* on *E. analoga* may be the only opportunity for successful larval metamorphosis. The percentage of fouled *E. analoga* (7.3%) appears important considering the density of sand crabs (about 65 ind m<sup>-2</sup>) in the study area. The abundance of *E. analoga* varies between 10 and 85 ind m<sup>-2</sup> (Arntz et al. 1987) and can reach maximum values of 111.6 ind m<sup>-2</sup> before EN (Tarazona et al. 1985). In southern Chile even much higher values of 1675 ind m<sup>-2</sup>, related to temporal variability in recruitment, were reported (Contreras et al. 1999).

Mainly juvenile mussels were attached to the crabs. Individuals of *S. algalus* in northern and central Chile (lat 30°) reach a maximum size exceeding 70 mm (González et al. 1980; Tokeshi and Romero 1995), are hermaphroditic with mature gametes during the entire year (González et al. 1980), and may obtain sexual maturity at 20 mm (Gallardo 2001). In the present study the maximum size of epibiotic *S. algalus* was a little smaller (17.4 mm). However, our study site was 1300 km north of the former study area and it is possible that in low latitudes the bivalves reach sexual maturity in smaller size classes (according to Thorson 1950). *S. algalus* on *E. analoga* are unlikely to commonly reach size necessary for reproduction. However, small mussels may colonize other substrates later on by detaching from the substrate and drifting elsewhere while larger individuals may undergo a lateral movement (Tokeshi and Romero 1995). Under favourable conditions and when more biogenous substrates for settlement are available (e.g. surf clams *M. donacium*), *S. algalus* may reach higher densities (Arntz 1987; Arntz and Fahrbach 1996), and epibiosis may facilitate the dispersal and contribute to gene flow of the rock mussel populations even more prominently.

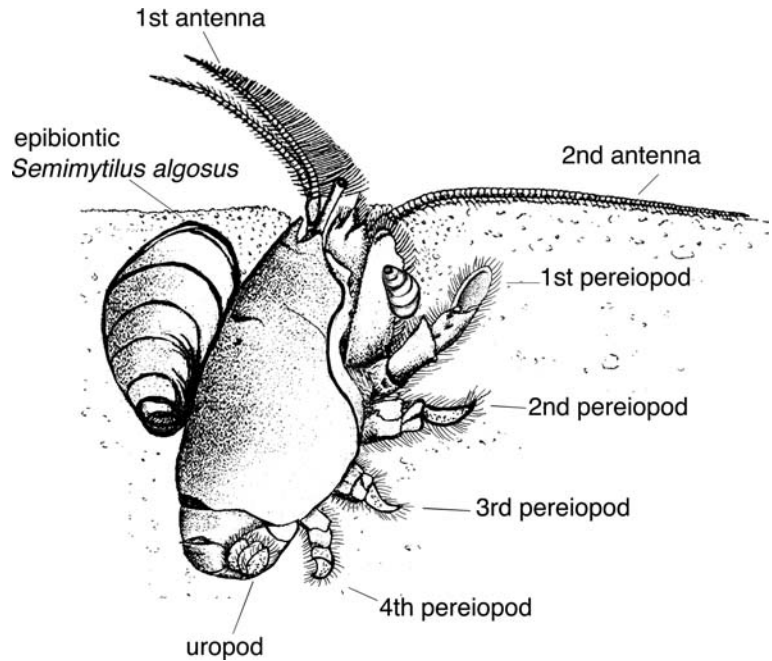
Epibiosis is apparently unfavourable for the basibiont. Fouling by calcareous epibionts causes an increase in mass, and therefore may reduce buoyancy (Wahl 1989). In the specific case of *E. analoga*, fouling is maximal on the anterior side (Fig. 5; zone 1, approximately 40%). The crabs are normally burrowed in the sand and only the anterior part of the carapace and the first appendices are exposed (Fig. 8; Ruppert et al. 2004; Dugan 2000). In this position, the sand crab filters and mussel larvae transported with the water current may be attracted by the hard surface and attach. On the other hand, mussel larvae might settle when crabs leave the sediment to undergo tidal migrations (Dugan et al. 2000). It is unknown why the right sides of the crabs were fouled more frequently than the left one. Maybe this can be explained by an asymmetrical use of the mouth tools or by the dominant current direction. However, to test these hypothesis further observations on the filtering behaviour and shallow subtidal current measurements are necessary.

Due to increased drag and mass the epibiont is likely to reduce the growth of the crabs (Wahl 1997) and might impact their migration behaviour. Furthermore, mechanical attachment of larger epibionts occasionally damages surfaces of the basibiont (Witman and Suchanek 1984; Wahl 1989).

In top-down controlled systems, epibiosis can strongly influence community dynamics, affecting many epibiont–basibiont–consumer interactions (Wahl 1989; Wahl et al. 1997; Laudien and Wahl 1999, 2004). In the western Baltic, for instance, the sea star *Asterias rubens* preys preferably on unfouled mussels (*M. edulis*) and the predation pressure decreases significantly when the mussels are fouled by hydrozoan and algae. This beneficial effect of fouling is known as associational resis-



**Fig. 8** Schematic drawing of a burrowed sand crab *E. analoga* fouled by the mussel *S. algosus*



tance (Laudien and Wahl 1999, 2004). However, in the case of the rock mussel–sand crab association, the opposite effect (‘shared doom effect’, Laudien and Wahl 1999) might occur when epibiotic individuals of larger size reduce the ability of *E. analoga* to escape from predators by increasing mass, reducing motility, and ultimately prolonging the burrowing time during the tidal migration (Dugan et al. 2000). A future study of the burrowing behaviour under predation pressure might give a deeper insight into the cost and benefits of this epibiosis between *S. algosus* and *E. analoga*.

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## References

Arntz WE, Brey T, Tarazona J, Robles A (1987) Changes in the structure of shallow sandy-beach community in Perú during an EL Niño event. In: Payne AIL, Gulland JA, Bink KH (eds) *The Benguela and comparable ecosystems*. S African J Mar Sci 5:645–658

Arntz WE, Fahrbach E (1996) NIÑO: Experimento climático de la naturaleza. Causas físicas y efectos biológicos. Fondo de la Cultura Económica Editores, Mexico

Caro AU, Castilla JC (2004) Predator-inducible defences and local intrapopulation variability of the intertidal mussel *Semimytilus algosus* in Central Chile. *Mar Ecol Prog Ser* 276:115–123

Contreras H, Defeo O, Jaramillo E (1999) Life History of *Emerita analoga* (Stimpson) (Anomura, Hippidae) in a sandy beach of south central Chile. *Estuar Coast Shelf Sci* 48:101–112

Conover MR (1979) Effect of gastropod shell characteristics and hermit crabs on shell epifauna. *J Exp Mar Biol Ecol* 40:81–94

Davis AR, Moreno CA (1995) Selection of substrata by juvenile *Choromytilus chorus* (Mytilidae): are chemical cues important? *J Exp Mar Biol Ecol* 191:167–180

Dugan JE, Hubbard DM, Wenner AM (1994) Geographic variation in life history of the sand crab, *Emerita analoga* (Stimpson) on the California coast: Relationships to environmental variables. *J Exp Mar Biol Ecol* 181:255–278

Dugan JE, Hubbard DM, Lastra M (2000) Burrowing abilities and swash behaviour of three crabs, *Emerita analoga* Stimpson, *Blepharipoda occidentalis* Randall, and *Lepidopa californica* Eford (Anomura, Hippoidea), of exposed sandy beaches. *J Exp Mar Biol Ecol* 255:229–245

Escribano R, Irribarren C, Rodríguez L (1997) Influence of food quantity and temperature on development and growth of the marine copepod *Calanus chilensis* from northern Chile. *Mar Biol* 128:281–288

Gallardo C (2001) Control de células neurosecretoras sobre el proceso gametogénico en *Semimytilus algosus* Gould, 1850 (Bivalvia: Mitilidae). Tesis para optar al título de Biólogo Marino. Facultad de Ciencias del Mar, Universidad Católica del Norte, Chile

Gili JM, Abelló P, Villanueva R (1993) Epibionts and intermolt duration in crab *Bathynectes piperitus*. *Mar Ecol Prog Ser* 98:107–113

González J, Villagra J, Hinojosa M, Becerra R (1980) Potencialidad del cultivo en balsa de *Semimytilus algosus* (Gould) 1850, en la Bahía de Concepción (Mollusca, Bivalvia, Mytilidae). *Boletim do Instituto Oceanográfico, Sao Paulo*. Sao Paulo 29:187–189

Jackson JBC (1977) Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *Am Nat* 111:743–767

Jaramillo E, McLachlan A, Coetzee P (1993) Intertidal zonation patterns of macrofauna over a range of exposed sandy beaches in South-central Chile. *Mar Ecol Prog Ser* 101:105–118

Jaramillo E, McLachlan A (1993) Community and population responses of the macrofauna to physical factors over a range of exposed sandy beaches in South-central Chile. *Estuar Coast Shelf Sci* 37:615–624

- Jaramillo E, Contreras H, Duarte C, Quijón P (2001) Relationships between community structure of the intertidal macroinfauna and sandy beach characteristics along the Chilean coast. *Mar Ecol* 22:323–342
- Laudien J, Wahl M (1999) Indirect effect of epibiosis on host mortality: Seastar predation on differently fouled mussels. *Mar Ecol* 20:35–47
- Laudien J, Wahl M (2004) Associational resistance of fouled blue mussels (*Mytilus edulis*) against starfish (*Asterias rubens*) predation: relative importance of structural and chemical properties of the epibionts. *Helgol Mar Res* 58:162–167
- Lutz RA, Kennish M (1992) Ecology and morphology of larval and early postlarval mussels. In: Gosling EM (ed) *The mussel Mytilus: ecology, physiology, genetics, and culture*. Dev aquacult fish science, vol 25. Elsevier, Amsterdam, pp 53–85
- Mann KH, Lazier JRN (1991) Dynamics of marine ecosystems Biological–physical interactions in the ocean. Blackwell Scientific Publications, Oxford
- Marín VH, Escribano R, Delgado LE, Olivares G, Hidalgo P (2001) Nearshore circulation in coastal upwelling site off the Northern Humboldt current system. *Cont Shelf Res* 21:1317–1329
- McLachlan A, Jaramillo E (1995) Zonation on sandy beaches. *Ocean Mar Biol Ann Rev* 33:305–335
- Mokady O, Arazi G, Bonar DB, Loya Y (1992) Settlement and metamorphosis specificity of *Lithophaga simplex* Iredale (Bivalvia: Mytilidae) on Red Sea corals. *J Exp Mar Biol Ecol* 162:243–251
- Navarrete SA, Broitman B, Wieters EA, Finke GR, Venegas RM, Sotomayor A (2002) Recruitment of intertidal invertebrates in the southeast Pacific: Interannual variability and the 1997–1998 El Niño. *Limnol Oceanogr* 47:791–802
- Olabarria C (2000) Epibiont mollusc on neogastropod shells from sandy bottoms, Pacific coast of Mexico. *J Mar Biol Ass UK* 80:291–298
- Perry DM (1980) Factors influencing aggregations patterns in sand crab *Emerita analoga* (Crustacea: Hippidae). *Oecologia* 45:379–384
- Ruppert EE, Fox RS, Barnes RP (2004) *Invertebrate Zoology—A functional evolutionary approach*, 7th edn. Brooks Cole/Thomson, Belmont, CA, pp 963
- Reusch T (1994) Factors structuring the *Mytilus*- and *Zostera*-community in the western Baltic: an experimental approach. PhD Thesis, University of Kiel, Kiel
- Sebens K (1985) The ecology of the rocky subtidal zone. *Am Sci* 73:548–557
- Schiedek D, Currie B (2004) Metabolic responses of two macrobenthic species to naturally occurring hydrogen sulphide. Southern African Marine Science Symposium (SAMSS 2002): Currents Coasts Communities
- Schwenke H (1969) Untersuchungen zur marinen Vegetationskunde. *Kieler Meeresforsch* 25:163–170
- Soto R (1985) Effects of the 1982–83 El Niño phenomenon on ecosystems of the I Region. *Invest Pesq (Santiago)* 32:199–206
- Stotz W, Lancellotti D, Lohrmann K, Von Brand E (2003) Replombamiento de bancos de Macha *Mesodesma donacium* en playa las machas de Arica, I Región, Chile. Proyecto FIP 2001–24, informe final
- Tarazona J, Arntz WE, Canahuire E, Ayala Z, Robles A (1985) Modificaciones Producidas durante “El Niño” en la Infauna Bentónica de Areas Someras del Ecosistema de Afloramiento Peruano. In: Arntz W, Landa A, Tarazona J. (eds) “El Niño” su Impacto en la Fauna Marina. Instituto del Mar del Perú
- Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biol Rev* 25:1–45
- Tokeshi M, Romero L (1995) Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore. *Mar Ecol Prog Ser* 119:167–176
- Wahl M (1989) Marine epibiosis I Fouling and antifouling: some basic aspects. *Mar Ecol Prog Ser* 58:175–189
- Wahl M (1997) Increased drag reduces growth of snails: comparison of flume and *in situ* experiments. *Mar Ecol Prog Ser* 151:291–293
- Wahl M, Mark O (1999) The predominantly facultative nature of epibiosis: experimental and observational evidence. *Mar Ecol Prog Ser* 187:59–66
- Warner GF (1997) Occurrence of epifauna on the periwinkle, *Littorina littorea* (L.), and interactions with the polychaete *Polydora ciliata* (Johnston). *Hydrobiologia* 355:41–47
- Witman JD, Suchanek TH (1984) Mussels in flow: drag and dislodgement by epizoans. *Mar Ecol Prog Ser* 16:259–268